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Population dynamics of muskrats in managed marshes at Delta, Manitoba

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by

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INTRODUCTION

Muskrats (<u>Ondatra zibethicus</u>) are an important component of wetland ecosystems, as well as being an economically important furbearer. Muskrats are the only significant resident vertebrate consumer of emergent vegetation in many North American wetlands. The large proportion of vegetation which they waste plays an important role in decomposition. Decomposing vegetation provides substrate for bacteria and fungi, which, in turn, feed increased populations of invertebrates (Godshalk and Wetzel 1978). Muskrat foraging and house-building improves interspersion in dense stands of emergent vegetation (Weller and Spatcher 1965, Weller and Fredrickson 1974) which increases invertebrate population levels and results in richer communities of invertebrates (Whitman 1974, Voigts 1976). Spatial interspersion of water and vegetation and increased invertebrate biomass in turn result in greater avian abundance, diversity, and waterfowl use in marshes (Weller and Spatcher 1965, Weller and Fredrickson 1974, Kaminski and Prince 1981). Muskrat houses provide nesting sites for Canada Geese (<u>Branta canadensis</u>) and resting places for other waterfowl (Perry 1982). Thus, the direct result of the muskrat's activities may be to increase the attractiveness of a marsh to waterfowl. However, populations of muskrats can exceed the carrying capacity of a marsh, "eating out" a marsh of emergent vegetation (O'Neil 1949).

Water level manipulation is used to manage wetland vegetation, invertebrates, and associated vertebrates. Drawdowns are used to restore emergent vegetation in barren shallow lakes (Kadlec 1962, Harris and Marshall 1963, van der Valk and Davis 1978). Overgrown marshes are flooded to thin less flood-tolerant plants toward a 50:50 interspersion of vegetation and water. Because of the association between muskrats, the characteristics of their wetland habitat, and water levels, knowledge of muskrat management is essential for implementing effective marsh management.

Muskrats readily invade newly-flooded marshes and, within 1 to 3 years, establish viable populations (Sooter 1946, Kroll and Meeks 1985). Aspects of muskrat population ecology have been studied since the 1930s (Errington 1938). Several researchers have contributed significantly to the knowledge of basic muskrat biology, ecology, and population dynamics (Sather 1958, Errington 1963, Mathiak 1966). Researchers have studied muskrat responses to different water levels, documenting differences in numbers of muskrat houses, population levels, and fur harvest. Some of these studies have documented the effects of drought (Seabloom and Beer 1964) and some the effects of fluctuating water levels (Errington 1937, 1938, Bellrose and Brown 1941, Bellrose and Low 1943). However, many of these studies have occurred under conditions of uncontrolled, fluctuating water levels on a single wetland (Olsen 1959, Errington et al. 1963, Proulx and Gilbert 1983). A few studies have compared differences in muskrat populations between marshes where water levels were controlled and uncontrolled (Bellrose and Brown 1941, Donohoe 1966) and there is general agreement that denser populations occur under conditions of stable water levels.

However, there are no controlled experiments documenting population responses of muskrats to different water-level manipulations. This study documents the responses of muskrat populations to three distinct water-level treatments in 10 artificially-managed marshes.

The first objective was to determine the effect of water levels on pre- and post-breeding muskrat population size presuming that muskrats will select habitat with optimum water depth. Deeper water could support a variety of emergent plants, provide security from mammalian and avian predators, and ensure access to food sources below surface ice in the winter.

The second objective was to determine the specific population parameters responsible for the observed dynamics. Population sizes are a function of rates of increase over the summer, survival rates, and carrying capacity of the habitat. Overwinter survival might be an especially critical parameter. Shallow marshes would be expected to freeze to the bottom in all but the mildest winters or under exceptional snow cover.

This condition would restrict muskrats from the food supply and decrease survival. If deeply-flooded marshes provide better habitat than shallowly-flooded marshes, this should be reflected by muskrats in better condition with greater rates of increase over the summer and increased survival rates.

METHODS

Study Area

Data were collected in the Marsh Ecology Research Project (MERP) cells at Delta Marsh, Manitoba (Batt et al. 1983). Delta Marsh is located at the south end of Lake Manitoba (50° 11′ N, 98° 19′ W) and covers about 180 km^2 of marsh and associated lowland (Hochbaum 1944). The local flora (Love and Love 1954, Walker 1959, Anderson and Jones 1976) and surrounding physiography (Elson 1967, Fenton 1970) have been well documented.

Ten adjacent ponds or cells, each about 5.5 ha, were constructed within a portion of the Delta Marsh. The cells are surrounded to the east, south and west by the main Delta Marsh. Lake Manitoba is located to the north across a narrow, wooded beach ridge. Cells were drawn down to mudflats for one year (cells 3 and 7) or two years (all other cells) prior to reflooding in early June 1985. During the drawdown period, the only water in the cells occurred in the borrow ditches excavated along the west edge of each cell. For a more detailed description of the construction and management of the MERP cells, see Murkin (1984).

Beginning in June 1985, water in the cells was maintained at three different levels: low (long-term average Delta Marsh level), medium (30 cm above average Delta Marsh level), and high (60 cm above average Delta Marsh level) (Fig. 1).

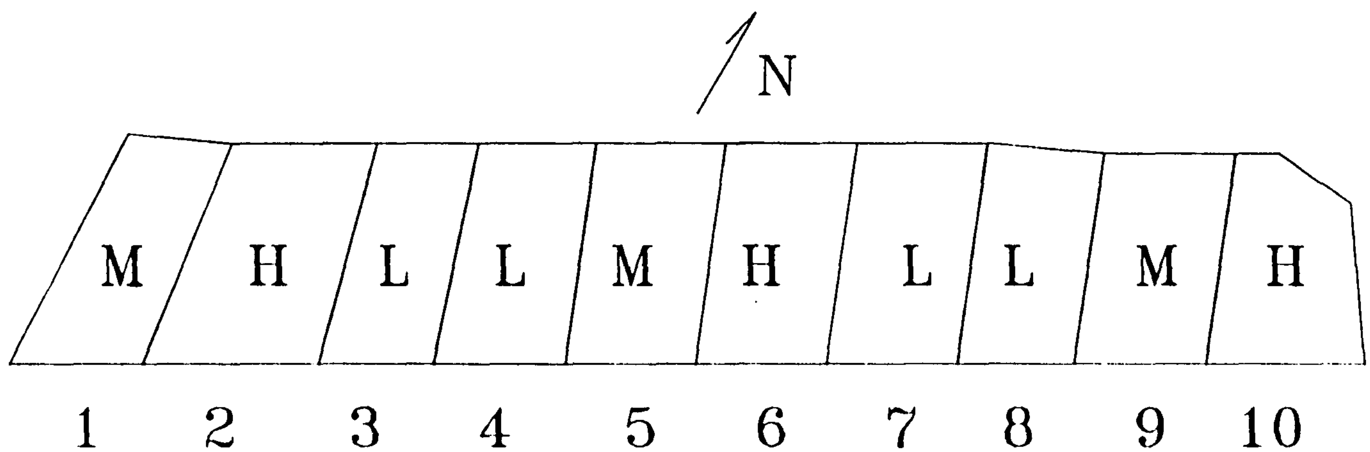

Figure 1. Arrangement of the cells and water-level treatments begun in 1985 (L = low, M = medium, H = high) in the Marsh Ecology Research Project at Delta Marsh, Manitoba

Topographic contours are such that the south end of the cells is generally deeper, progressing to dry land at the north end. Low cells are vegetated predominantly by whitetop (Scolochloa festucacea), common reedgrass (Phragmites australis), and cattail (Typha glauca). The medium and high cells are more predominantly cattail and bulrush (Scirpus spp.).

Trapping Methods

Muskrat populations were sampled during five periods: September 18 to October 28, 1985, April 20 to May 29, 1986, September 16 to October 22, 1986, April 21 to May 25, 1987, and September 1 to October 15, 1987. Hereafter, these periods will be referred to as October 1985, May 1986, October 1986, May 1987, and October 1987 respectively. A grid of 45 unbaited Tomahawk live traps (15.2 cm by 15.2 cm by 61.0 cm) spaced approximately 40 m apart was set for 6 consecutive days in each cell during each sampling period. Where a trap site occurred on dry land, the trap was set on the ground. At wet sites, traps were suspended at water level from wooden stakes. All traps were covered with vegetation from the surrounding area.

Captured animals were restrained in a handling cone (McCabe 1982) and marked with two, uniquely-numbered, #1 monel eartags (National Band and Tag Company, Newport, Kentucky). Date of capture, cell and trap location, body weight to the nearest 25 g, body length (nose to base of tail) to the nearest 5 mm, hindfoot length to the nearest 1 mm, and sex were recorded.

Field aging was based on body-weight growth curves constructed by Olsen (1959:43) for muskrats at Delta Marsh. From this information, I interpreted that muskrats 4-5 months old at Delta Marsh weighed an average of 750-800 gms. Because the oldest juvenile muskrats I caught in fall were probably only 4.5 months old, I classified muskrats as juveniles up to a weight of 750 gm and as adults if they were heavier.

Usually, 2 cells were trapped simultaneously. The order in which cells were trapped was randomly assigned during each trapping period and all 10 cells were trapped within 6 weeks. During the period of this study, no kill trapping was allowed within the MERP cells or within 800 m of the project.

Population Estimates

Models for closed populations (Otis et al. 1978) were used to estimate population size in each cell ($\hat{N}_i$) during period i. In selecting the appropriate model, I considered; 1) the capture probabilities and the results of the experiments, 2) the model selection procedure used by CAPTURE, and 3) the simulations of bias and precision given by Otis et al. (1978).

Estimating Survival

Survival was estimated using a capture-recapture design described by Pollock (1982), in which two types of sampling periods are defined. Primary periods were October or May trapping periods while the secondary periods were each of the 6 days during which a cell was trapped within a primary period. The secondary sampling periods were "pooled" so that the trap record simply indicates whether an animal was captured or uncaptured during a primary period. Jolly-Seber (Seber 1982:199-202) estimates of survival between primary periods were generated with the computer program POPAN-2 (Arnason and Baniuk 1978). Overwinter refers to the 7-month interval between the October and May trapping periods while oversummer refers to the 5-month interval between the May and October trapping periods. An estimator of the survival rate from period i to i+1 is,

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{(\hat{M}_i - m_i + R_i)}$$

with variance,

$$V(\hat{\phi}_i) = \hat{\phi}_i^2 \left\{ \frac{(\hat{M}_{i+1} - m_{i+1})(\hat{M}_{i+1} - m_{i+1} + R_{i+1})}{\hat{M}_{i+1}^2} \left(\frac{1}{r_{i+1}} - \frac{1}{R_{i+1}}\right) + \frac{\hat{M}_i - m_i}{\hat{M}_i - m_i + R_i} \left(\frac{1}{r_i} - \frac{1}{R_i}\right) + \frac{1 - \hat{\phi}_i}{\hat{M}_{i+1}} \right\},$$

where $\hat{M}_i$ is the number of marked animals in the population before the ith sample, m_i is the number of marked animals caught in the ith sample (of size n_i), R_i is the number of the n_i animals that are released, of which r_i are subsequently recaptured. Daily survival rates were calculated by taking the Lth root of $\hat{\phi}_i$, where L is the number of days in the interval between trapping periods.

Estimating Finite Increase

Percent finite rates of increase from time i to i+1 were calculated for each cell for the periods May to October 1986 and May to October 1987 by,

$$\%\hat{F}I = \frac{(\hat{N}_{i+1} - \hat{N}_i)}{\hat{N}_i} (100)$$

with variance,

$$V(\%\hat{F}I) = \%\hat{F}I^2 \left[\frac{V(\hat{N}_{i+1})}{\hat{N}^2_{i+1}} + \frac{V(\hat{N}_i)}{\hat{N}^2_i} - \frac{2 \text{ Cov}(\hat{N}_i, \hat{N}_{i+1})}{(\hat{N}_i)(\hat{N}_{i+1})}\right],$$

where $\hat{N}$ is the population estimate for the appropriate time period. Percent finite rates of increase were correlated with ln (May $\hat{N}$) for both years.

Body Condition

An index of body condition was estimated for each animal caught for which I had both a measurement of body length and of body weight (Willner et al. 1979). The formula for body condition index was:

$$\mathrm{BCI} = \frac{\text{body weight (kg)}}{\text{body length (m)}^3}.$$

Condition indices were calculated for adults and juveniles in each cell for each of the 5 trapping periods. Average BCI of juveniles and adults was calculated for each cell in each trapping period. Only averages derived from 5 or more animals were used in correlation analyses.

Overwinter Weight Change

Weight changes during each winter were calculated for muskrats caught in October and again the following May. The weight change was the difference in grams between the May weight and the previous October weight measured to the nearest 25 g.

Movements

Movement rates of animals among cells between trapping periods were calculated for each individual that was captured during more than one trapping period. The movement rate ($MR_{i,j}$) out of a cell (j) between periods i and i+1 was determined by the formula,

$$MR_{i,j} = \frac{\sum_{n=1}^{10} m_{i+1,n} \mid n \neq j}{\sum_{n=1}^{10} m_{i+1,n}},$$

dividing the number of recaptures in a cell other than the jth by the total number of recaptures in all 10 cells.

Statistics

All among-treatment tests of difference were performed using analysis of variance (ANOVA) with an error term of the variation among cells within a treatment. Associations between $\overline{BCI}$, $\%\widehat{FI}$ and $\hat{N}$ were tested using simple linear regression. Non-parametric chi-square tests were used to determine differences in movement rates among treatments. The expected rates of movement were obtained by multiplying the proportion of the total muskrat population in a water-level treatment by the availability of the water-level treatment to which they were moving to.

Unless otherwise noted, all means are plus or minus 1 standard error of the mean.

RESULTS

Population Estimates

In five sampling periods, 2522 animals were caught. Of these, only 20 or 0.8 % were caught in more than one cell during the 6 weeks of any spring or fall sampling period. In tests performed by CAPTURE (Otis et al. 1978), only 6 out of 48 populations rejected tests of closure. This evidence supports the assumption of geographical closure within primary periods.

Model M_{bh} (Otis et al. 1978), assuming heterogeneous capture probability and behavioral trap responses, was used to estimate N in all cells. This model was selected as best by the program CAPTURE in 8 out of 48 possible estimates. Model M_h was actually selected more frequently by CAPTURE, but simulation results (Otis et al. 1978:130) suggest better performance of M_{bh} with parameters in the observed ranges. Capture probabilities averaged 0.34 and M_{t+1} ranged from 2 to 146, averaging 53 within 6-day trapping regimes. In simulation trials based on models M_{bh} and M_h with similar parameters, estimated 95% confidence intervals on $\hat{N}_{bh}$ included the real population size in 78% of the trials. In the case of model M_h, the estimated 95% confidence interval included the real population size in 44% of the trials in one example (with an average population estimate above the real population size) and in 77% of the trials (with an average population estimate below the real population size) in another example. In all but one simulation using model M_{bh}, bias was consistently negative, ranging from 3% to 15%. Otis et al. (1978) proposed there was no serious bias in the population estimate if relatively few of the actual population remained untrappable, and trapping records show a decrease in the number of unmarked animals captured over time. Computer simulations with model M_h resulted in absolute bias ranging from 0% to 17% but Otis et al. (1978) were unable to generalize about the positive and negative bias.

The use of only one estimation model for all cells and seasons facilitates comparison among cells, treatments, and years without introducing unnecessary variation into the experimental design with different estimators. Although this model may generate a somewhat conservative estimate, with the high capture probabilities I believed that the estimated population size was realistic. Model M_h gave more variable results and appeared to overestimate population size when large numbers of animals were caught.

Table 1 summarizes the number of animals caught during each trapping period, the resulting population estimates, and capture probabilities. Notice that M_{t+1} closely approximates $\hat{N}$ in cells with high capture probabilities suggesting that, in many cases, nearly all muskrats residing in a cell were captured. Mean population estimates among water-level treatments were not different ($\underline{F}$ = 1.72, $\underline{P}$ = 0.247) although

Table 1. Number of muskrats captured (M_{t+1}), average probability of capture ($\hat{p}$), population estimates ($\hat{N}$), and standard errors ($\widehat{SE}$) in each MERP cell during 1985 through 1987 at Delta Marsh, Manitoba

		Oct 1985				May 1986				Oct 1986				May 1987				Oct 1987			
Cell	Water Level	M_{t+1}	$\hat{p}$	$\hat{N}$	$\widehat{SE}$	M_{t+1}	$\hat{p}$	$\hat{N}$	$\widehat{SE}$	M_{t+1}	$\hat{p}$	$\hat{N}$	$\widehat{SE}$	M_{t+1}	$\hat{p}$	$\hat{N}$	$\widehat{SE}$	M_{t+1}	$\hat{p}$	$\hat{N}$	$\widehat{SE}$
1	Med	41	0.48	41	1.13	20	0.51	20	0.61	92	0.31	103	6.39	45	0.46	46	1.34	106	0.22	136	15.23
2	High	49	0.53	49	0.82	26	0.67	26	0.03	146	0.30	164	8.29	37	0.49	38	2.32	131	0.32	145	7.08
3	Low		not trapped			8	0.42	8	0.75	69	0.29	79	6.38	45	0.31	64	25.81	91	0.24	112	11.47
4	Low	12	0.67	12	0.13	11	0.46	11	0.67	47	0.33	51	3.89	46	0.55	46	0.71	69	0.25	83	9.12
5	Med	2	1.00	2	0.001	13	0.52	13	0.46	66	0.35	71	3.89	54	0.63	54	0.40	105	0.33	115	5.68
6	High	2	0.67	2	0.05	6	0.38	6	0.92	67	0.39	70	2.70	30	0.51	30	0.77	102	0.19	140	20.82
7	Low		not trapped			2	1.00	2	0.001	46	0.26	55	6.98	36	0.41	37	1.82	42	0.17	62	18.38
8	Low	29	0.50	29	0.81	6	0.50	6	0.37	95	0.22	123	15.20	32	0.54	32	0.62	88	0.27	103	8.46
9	Med	32	0.46	32	1.14	24	0.53	24	0.57	117	0.25	142	12.08	56	0.44	57	1.78	114	0.25	139	12.30
10	High	21	0.49	21	0.75	14	0.52	14	0.49	93	0.26	111	9.72	32	0.57	32	1.03	104	0.21	137	17.42

among season differences were highly significant (F = 69.47, P < 0.001) according to ANOVA (Fig. 2).

Survival

Estimates of survival ($\hat{\phi}_i$) were calculated for each cell over 3 intervals: October 1985 to May 1986, May to October 1986, and October 1986 to May 1987. ANOVA indicated daily survival estimates were not different among treatments (F = 1.35, P = 0.318) or among intervals (F = 1.85, P = 0.203) (Table 2). The daily survival rate of muskrats in cell 6 for the period from May to October 1986 was much lower than any other estimate. When this estimate was dropped as an outlier, the average daily survival rate was 0.9976 (SE = 0.0007). Survival estimates were still not different among treatments (F = 0.20, P = 0.822) but were then different among intervals (F = 16.45, P < 0.001). Daily survival rates for the October to May intervals were lower than the May to October interval. Monthly survival rates were 0.87, 0.93 (excluding cell 6), and 0.84 for periods October 1985 to May 1986, May to October 1986, and October 1986 to May 1987, respectively. The annual survival rate from October 1985 to October 1986 was 0.27.

Finite Increase

Average %$\hat{FI}$ (Table 3) was significantly different between May to October intervals (F = 12.67, P = 0.009). When both May to October intervals were analyzed separately, %$\hat{FI}$ in 1986 was not different among treatments (F = 1.99, P = 0.206) while

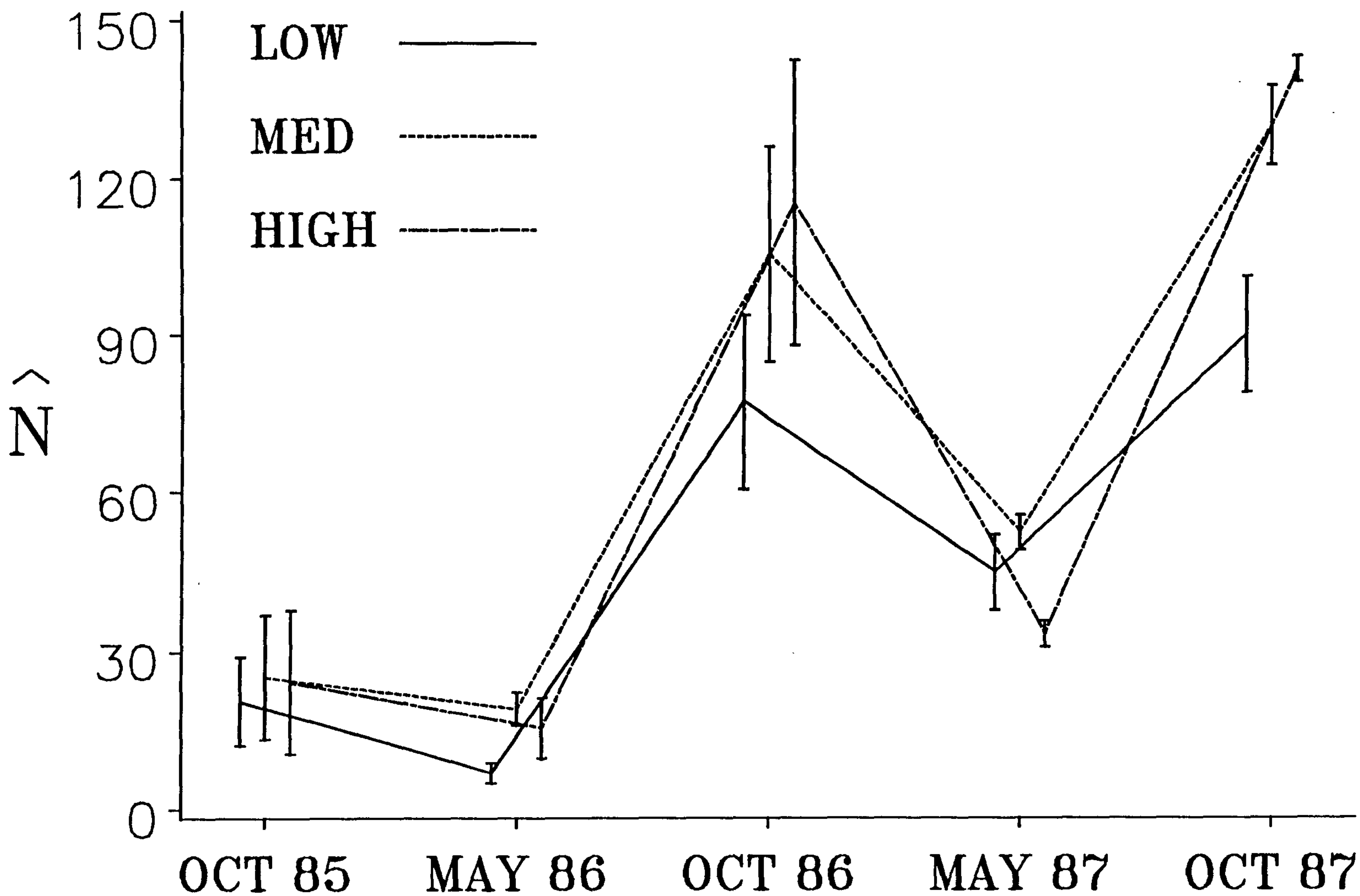

Figure 2. Average population estimates (± 1 SE among replicates) for each water-level treatment in the MERP cells at Delta Marsh, Manitoba from 1985-1987

Table 2. Daily survival of muskrats averaged across all cells ($\bar{\phi}_i$) and standard errors (SE) during 1985 to 1987 at Delta Marsh, Manitoba

Interval	$\bar{\phi}_i$	SE
Oct 1985 - May 1986	0.9953	0.0007
May 1986 - Oct 1986	0.9966	0.0012
Oct 1986 - May 1987	0.9943	0.0006

Table 3. Percent spring to fall increase (%FI) and standard error among replicates (SE) of muskrat populations in each water-level treatment in the MERP cells at Delta Marsh, Manitoba, 1986 through 1987

Water Level	No. Cells	1986 $\widehat{\%FI}$	1986 $\widehat{SE}$	1987 $\widehat{\%FI}$	1987 $\widehat{SE}$
Low	4	1462.8	515.3	111.2	37.0
Medium	3	450.9	22.3	150.8	24.1
High	3	763.4	158.7	325.5	24.6
Mean	10	949.4	241.4	187.4	34.6

$\%\hat{FI}$ in 1987 was different among treatments (F = 12.55, P = 0.005).

The $\%\hat{FI}$ for May to October 1986 was negatively correlated with ln $\hat{N}$ in May 1986 (r^2 = 0.751, P < 0.001) (Fig. 3). The $\%\hat{FI}$ for May to October 1987 was also negatively correlated with ln $\hat{N}$ in May 1987 (r^2 = 0.469, P = 0.017) (Fig. 4).

Body Condition

Body condition index of adults was not different among treatments (F = 2.37, P = 0.164) but was significantly different among the 5 trapping periods (F = 22.93, P < 0.001) (Table 4). When $\overline{BCI}$ of juveniles and adults in October was compared, there was no effect of water-level treatment (F = 0.92, P = 0.441) but there were differences between age (F = 121.00, P < 0.001) and among trapping periods (F = 46.80, P < 0.001) (Table 4).

Average $\overline{BCI}$ of adults was negatively correlated with $\hat{N}$ in each cell from all 5 trapping periods (r^2 = 0.366, P < 0.001) (Fig. 5). Average $\overline{BCI}$ in fall was negatively correlated with $\hat{N}$ in each cell for both juveniles (r^2 = 0.257, P = 0.007) and adults (r^2 = 0.268, P = 0.006) (Fig. 6).

Overwinter Weight Change

Three hundred forty-three measurements of overwinter weight change were documented during the 2 winters. Of these, 97% (331 animals) had gained weight. Overwinter weight gain was different between the 2 winters (October to May intervals)

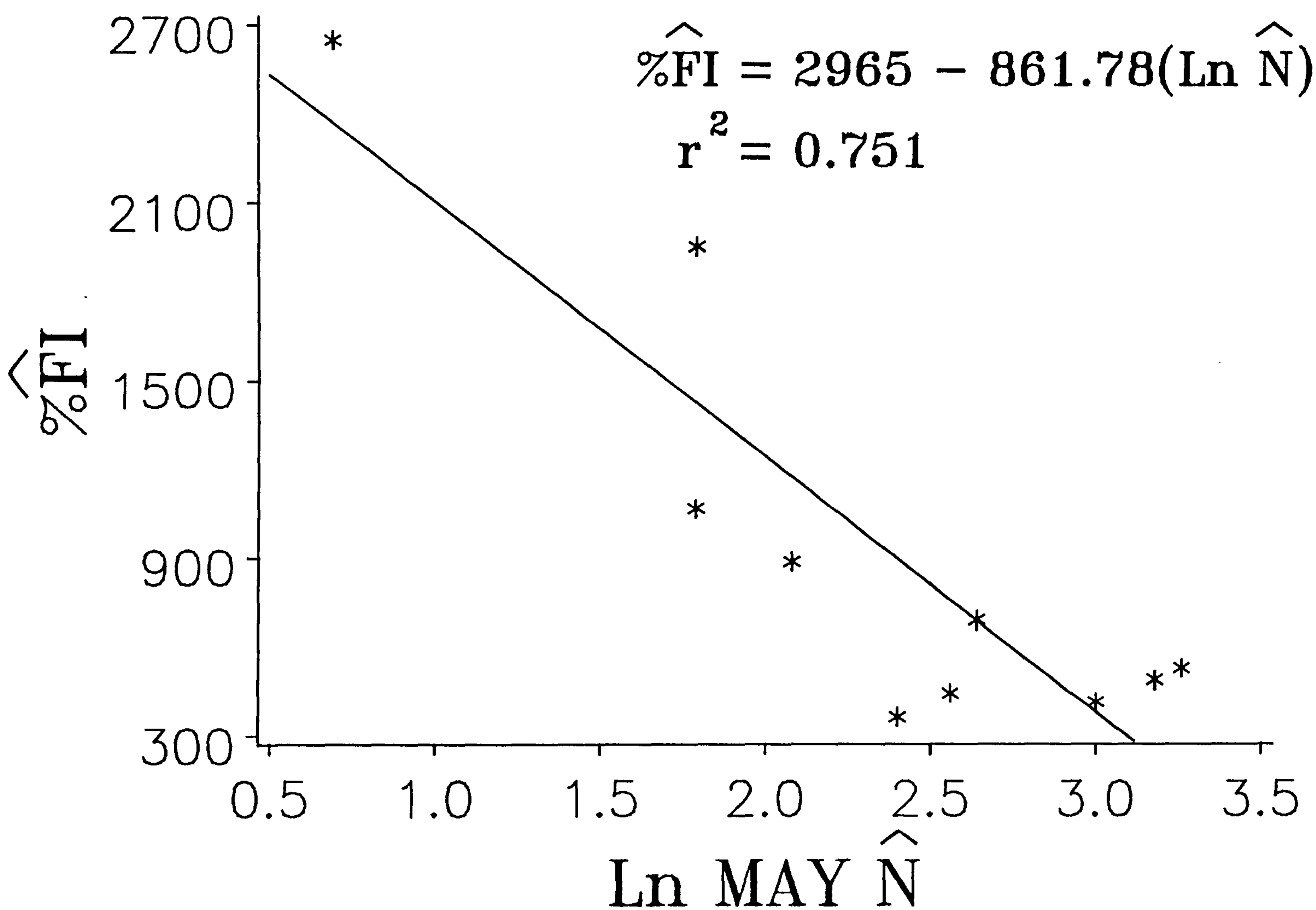

Figure 3. Percent spring to fall increase ($\widehat{\%FI}$) in 1986 as a function of the logarithm of the spring population size ($\hat{N}$) in the MERP cells at Delta Marsh, Manitoba

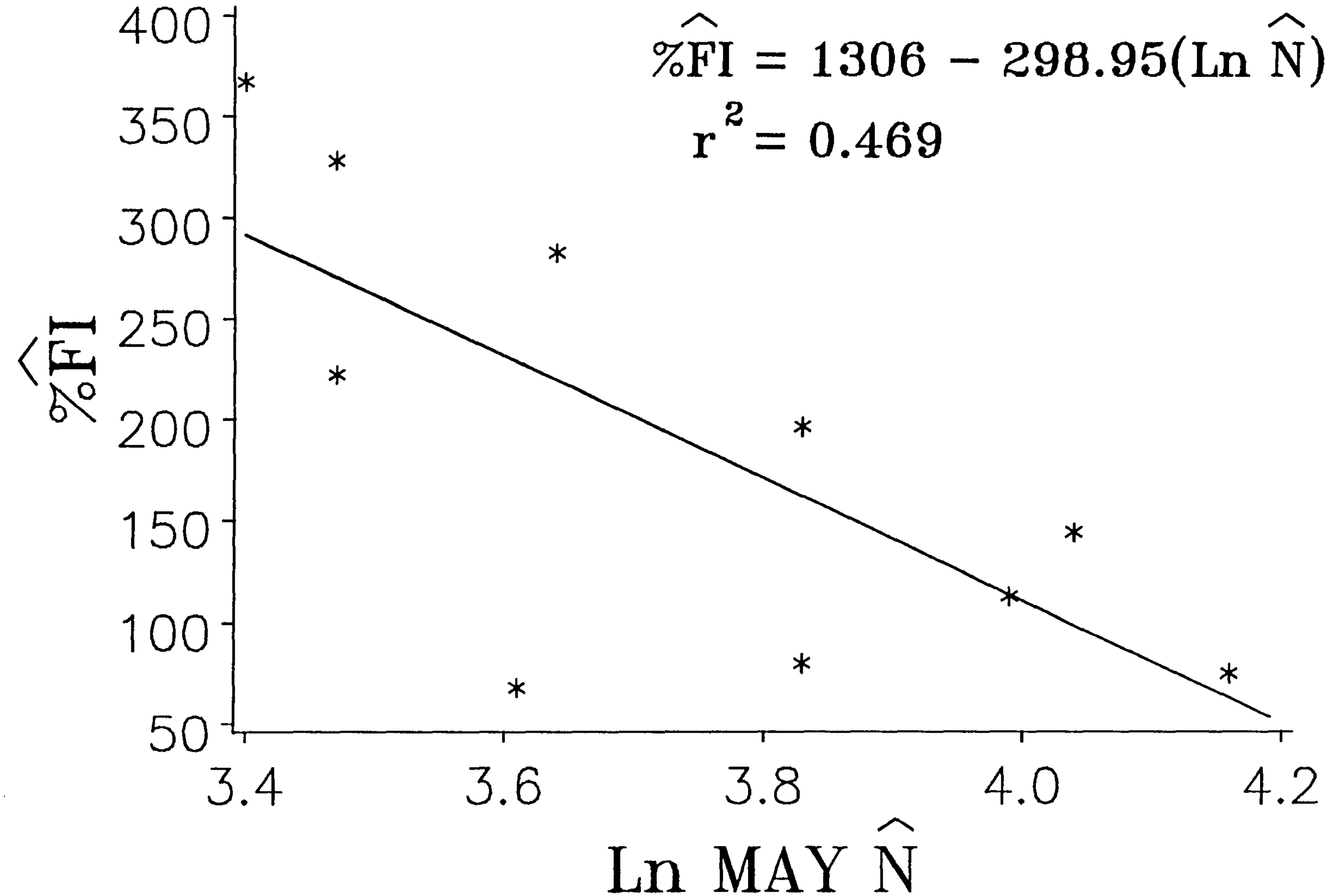

Figure 4. Percent spring to fall increase ($\widehat{\%FI}$) in 1987 as a function of the logarithm of the spring population size ($\hat{N}$) in the MERP cells at Delta Marsh, Manitoba

Table 4. Average body condition index ($\overline{BCI}$) and standard errors (SE) of muskrats caught in the MERP cells at Delta Marsh, Manitoba, 1985 through 1987

	Juveniles		Adults	
Trapping Period	$\overline{BCI}$	SE	$\overline{BCI}$	SE
Oct 1985	38.3	0.6	38.5	0.9
May 1986			41.5	0.6
Oct 1986	33.8	0.2	36.6	0.3
May 1987			38.8	0.3
Oct 1987	33.9	0.2	36.9	0.3

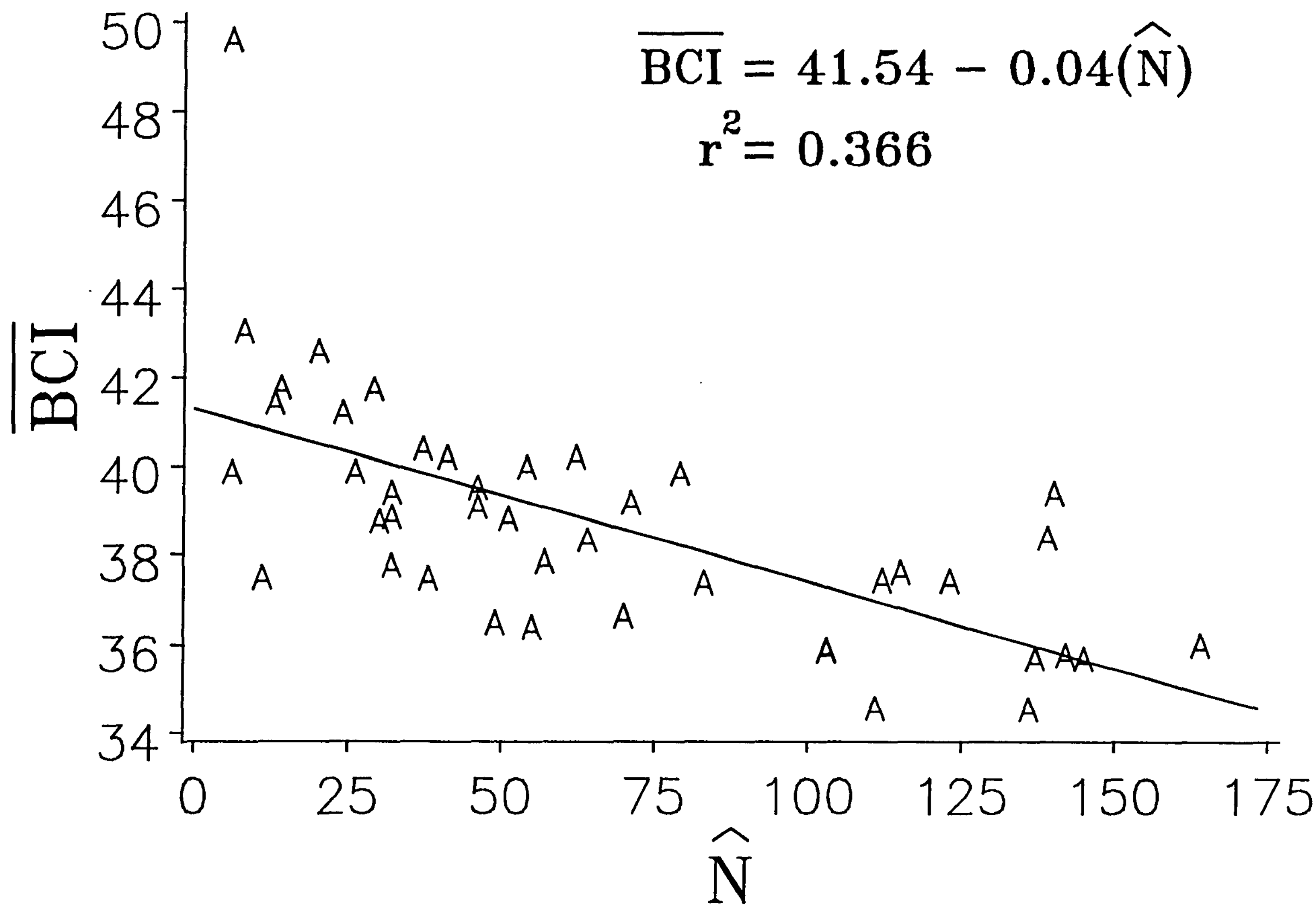

Figure 5. Correlation of body condition ($\overline{BCI}$) of adult muskrats with population size ($\hat{N}$) in the MERP cells at Delta Marsh, Manitoba, in all seasons, 1985 through 1987

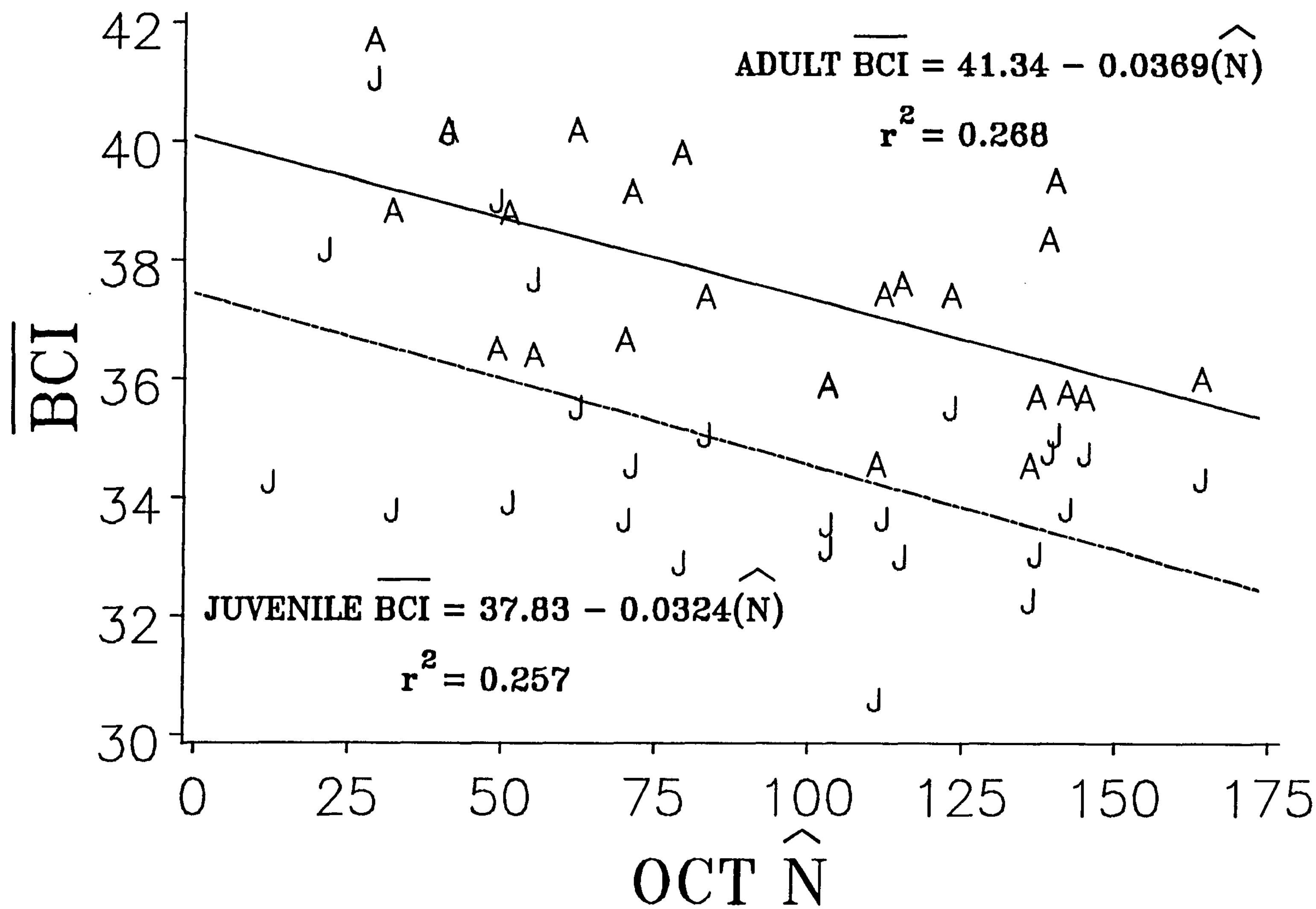

Figure 6. Correlations of body condition ($\overline{BCI}$) of adult and juvenile muskrats on population size ($\hat{N}$) in the MERP cells at Delta Marsh, Manitoba, from 1985 through 1987

(F = 14.51, P < 0.001) and between ages (F = 85.02, P < 0.001), but was not affected by water-level treatments (F = 1.74, P = 0.244) (Table 5). Juveniles gained 53% more weight than adults the first winter and 69% more the second. Weight gains were reduced the second winter by 10% for juveniles and 18% for adults.

Movements

Rates of movement among cells were not different between the 2 years (X^2 = 0.113, P = 0.710). In the first year, movement rates between October and May (41%) were significantly greater than between May and October (9%) (X^2 = 18.856, P < 0.001). Results were similar in the second year with movement rates between October and May (36%) greater than between May and October (6%) (X^2 = 52.086, P < 0.001).

Animals that moved out of a cell could move to a cell with the same water-level treatment (e.g., low to low) or to cells with one of the other 2 treatments (e.g., low to medium or low to high). Using data pooled from both winters, statistical tests indicated that movements among treatments were not random (X^2 = 23.027, P = 0.003). Movements from low cells to medium cells occurred 2.1 times as often as would be expected, and movements from high cells to other high cells occurred only 0.4 times as often as would be expected.

Table 5. Average overwinter weight gain (g) and standard errors (SE) of muskrats in the MERP cells at Delta Marsh, Manitoba, 1985 through 1987

	Juveniles		Adults	
Time Period	Gain	SE	Gain	SE
Oct 1985 - May 1986	385	17	250	36
Oct 1986 - May 1987	348	8	205	18

DISCUSSION

Population Size

The rapid increase of muskrat populations in the MERP cells over the first 2 years is typical of muskrat populations elsewhere (Errington et al. 1963, Palmisano 1972, Danell 1978, Kroll and Meeks 1985). When the cells were drawn down, it is possible that a few muskrats remained resident in the borrow ditches. However, all cells have similar borrow ditches so that the effect was consistent across all cells. Most muskrats must have migrated into the cells during the summer of 1985, as they are capable of doing (Errington 1943, Errington et al. 1963, Kroll and Meeks 1985).

Densities of muskrats in 1985 through 1987 ranged from 0.3/ha to 27.2/ha. These densities are greater than reported by Clay and Clark (1985) along the Mississippi River, where densities ranged from 0.3/ha to 9.3/ha. Gashwiler (1948) found the greatest densities of muskrats in a marsh in Maine to be only 3.9/ha. The upper range of the density estimates from MERP closely resemble density estimates made by Proulx and Gilbert (1983) of up to 22.6/ha. My estimates are less than some Iowa marshes where Errington (1948) reported winter densities as great as 86/ha in cattail, with 49/ha being more normal. After large increases initially, October populations in 1987 were only slightly greater than those of 1986 suggesting that population levels may be reaching carrying capacity.

Although population estimates were not different among treatments, some trends were apparent. Annual increases of populations from May to October and decreases from October to May occurred in all treatments. However, populations in cells with low water levels do not appear to be increasing as rapidly or decreasing as drastically between trapping periods. Populations in the high and medium water-level treatments seem to decrease more and reach greater peaks. This difference was not statistically detectable until the October 1987 experiments, but it appears that population dynamics among water-level treatments may diverge within the next few years. At this point, I conclude that deeper marshes do not produce denser populations of muskrats than shallow marshes.

Survival Rates

Low water levels may expose more muskrats to avian and mammalian predation. While they are active, muskrats spend most of their time feeding (Welch 1980). If they forage in shallow water or near shore, they are more exposed to predation. During this study, mink (*Mustela vison*) were sometimes caught in muskrat traps, invariably in traps set in shallow water. It is possible, therefore, that deeper marshes offer more protection from predation. In this study, it was impossible to separate mortality due to predation from other causes of mortality so no comparison among treatments could be made.

Care should be taken when comparing survival rates with other studies because estimates are often not consistent with regard to age and time intervals. Average monthly winter survival rates in MERP were less than those suggested by data from Proulx and Gilbert (1983) from southern Ontario, but greater than the rate of 0.82 found by Clay and Clark (1985) on the Mississippi River.

Monthly summer survival rates compared in a similar fashion; less than the rates suggested by data from Ontario (Proulx and Gilbert 1983) and greater than the rate of 0.84 for both juveniles and adults on the Mississippi River (Clay and Clark 1985).

Annual survival was greater than the rate of 0.13 reported by Clay and Clark (1985) on the Mississippi River and 0.13 reported by Mathiak (1966) over 11 years at Horicon Marsh, Wisconsin. Clay and Clark (1985) reanalyzed Mathiak's (1966) data and concluded an annual rate of 0.16. Clark (1987) separated survival rates between birth year (BY) and after birth year (ABY) animals. Annual survival rates were 0.16 for BY animals and 0.06 for ABY animals. All these rates are less than the rate of 0.27 calculated in my study.

The muskrat populations at MERP were newly established and still increasing so that higher survival rates would be expected compared to populations that had persisted for a longer time. The summer survival rate is higher than both winter survival rates reflecting the harshness of the winter environment. The survival rate in the second winter (with higher populations) was less than in the first winter (with lower populations) which is consistent with density dependent responses in population dynamics.

Other studies have shown that fluctuating water levels can contribute to increased mortality among muskrats (Bellrose and Low 1943, Donohoe 1966, Proulx and Buckland 1986). Stable water levels reduce migration necessary to avoid unsuitable habitat, which in turn reduces mortality (Shanks and Arthur 1952, Sather 1958, Arata 1959). I believe the most important fact in determining survival was the stable water level, with minimum depths in all cells sufficient for muskrat use (Perry 1982), rather than the relative water depths used as treatments in this study. In this case, deeper water did not increase survival. This would concur with the findings of Bellrose and Brown (1941).

Population Increase

Many studies of muskrats have found spring to fall increase or direct measures of reproduction to be density dependent. Beer and Truax (1950) and Errington (1961) noted highest rates of increase among muskrats at low densities. Rates of increase were much higher during 1986 when population levels were lower than in 1987 after populations in the MERP cells had increased. This, together with decreasing overwinter survival rates as populations increase, could contribute to the declining rate of population growth in the MERP cells.

Body Condition and Overwinter Weight Gain

The inverse relationship between body condition and population size I noted was similar to that found by Angerbjörn (1986) among mountain hares. Angerbjörn (1986) also found that an increased number of young were produced with females of higher body condition. He concluded that the density dependent increase in reproduction was mainly due to changing body conditions. However, both Clay (1983) and I found no correlation between reproductive rates and body condition.

No studies of which I am aware have documented weight gain of individual muskrats overwinter. In contrast to previous studies at Delta Marsh (Olsen 1959), juvenile muskrats gained significant weight overwinter. Several other studies have calculated rates of weight change by comparing the relative weights of adults and juveniles in spring with those of fall animals (Olsen 1959, Friend et al. 1964). Friend et al. (1964) concluded that normal overwinter weight loss was 16%; lowering water levels during the winter increased the weight loss. The rates of growth measured in this study are not as great as growth rates measured for juveniles over the summer (Dorney and Rusch 1953, Olsen 1959, Parker and Maxwell 1980, 1984). However, winter conditions under the ice and in burrows and lodges are apparently not so severe that growth cannot take place. MacArthur and Aleksiuk (1979) found that muskrat lodges could be 30° C warmer in winter than ambient air temperature. They suggested that energy costs for thermoregulation were minimized through construction and selective use of lodges. Provided that sufficient water depths and vegetation exist to ensure access to food, there is apparently no reason that muskrats, especially juveniles, should not continue to grow through the winter. Considering the short length of northern summers, this would seem to be an important adaptation of the species.

Movements

Movements among cells confounded my ability to independently estimate survival using Jolly-Seber methods. Movements among cells within the May and October trapping periods were negligible, in spite of the fact that it took 6 weeks to complete the experiment. Furthermore, muskrats were very sedentary during the summer. Neal (1968) reported that most summer home ranges of muskrats at Rush Lake could be enclosed within a circle 46-61 m in diameter. Clay and Clark (1985) recaptured most individuals within 50 m of the original capture site. Despite the fact that MacArthur (1978) found most mid-winter locations of radio-tagged muskrats on the

Delta Marsh to be within 15 m of their lodge, overwinter movement rates in the MERP cells were significantly greater than summer movements. It appears that sometime between the end of October and mid-April, a substantial number of muskrats moved to another cell. There is no doubt that the close proximity of the cells to each other facilitated this. Dispersal in muskrats is associated with spring and the onset of ice break-up (Sather 1958, Errington 1963, Errington et al. 1963) and it is likely that this is when movement occurred among the MERP cells.

Being able to directly estimate the dispersal rate would allow me to estimate survival more accurately. Zeng and Brown (1987) proposed a method for distinguishing dispersal from death in mark-recapture studies. However, an important assumption of their method is that distribution of habitat is uniform throughout the area. Observations of muskrats and their lodges in the main part of the Delta Marsh confirm that habitat within the MERP cells is much more attractive to muskrats than is the majority of the Delta Marsh. From aerial photos of the Delta Marsh, it is obvious that vegetation interspersion in the MERP cells more closely typifies the hemi-marsh stage described by Weller and Spatcher (1965) than does the main marsh. Olsen (in Errington 1963:596) observed fall densities of 8.4 muskrats/ha in the Delta Marsh. These lower densities probably reflect the poorer habitat quality of the main marsh as compared to the MERP cells. Kroll and Meeks

(1985) noted that muskrats readily moved into managed marshes with predominantly cattail vegetation.

Some researchers have noted 2 periods of dispersal, spring and fall (Shanks and Arthur 1952, Parker and Maxwell 1980). Parker and Maxwell (1984) conservatively estimated a fall to spring dispersal rate of 11% out of 3 managed ponds. Arata (1959) concluded that fall movement was probably induced by low water conditions although Errington (1939) noted fall migrations during years of normal water levels. If low water levels induced movement in MERP, one would expect that the majority of movements would be from low cells to medium and high cells. However, only the low to medium movements were greater than expected. Habitat selection, especially the influence of vegetation species and structure, must play an important role in dispersal.

High population pressures can force muskrats to move out of familiar marshes (Errington 1951), although it is unlikely that such pressures could account for the movements observed. Population levels in October of 1985 were much less than in October of 1986, yet movement rates were not significantly different between years. Population levels in all water-level treatments continued to increase into 1987 suggesting that available habitat was not yet at carrying capacity. Thus movements from low water cells or into deeper cells is not explainable based on density alone.

The MERP cells provide an atypical situation where muskrats can easily move from one habitat to another with a good chance of survival. More typically, muskrat migrations result in mortality (Shanks and Arthur 1952, Sather 1958). Errington (1943) stated that many migrating muskrats fall prey to mink. Muskrats are relatively safe during the open-water season as long as they remain within the security of the marsh. Mink scats collected near Minnedosa, Manitoba contained large amounts of muskrat remains (as high as 56.8%) (Arnold and Fritzell 1987) especially early in spring when frozen marshes provide access to muskrat lodges and mink have few alternative prey. Low water levels in Ontario provided access for mink to the center of the marsh during some summers (Proulx et al. 1987), and muskrat remains in mink scats were as high as 39% during these periods.

Thus dispersing muskrats typically face territories already occupied, increased chance of predation, and unknown habitat conditions. In most cases, a dispersing muskrat is a dead muskrat. In terms of the MERP experiment, it matters little if the muskrat died within a cell or left a cell because of poor habitat conditions, it still represents a loss related to water level effects.

Management Implications

The MERP studies give reason to evaluate some current water-level management of wetlands. Trappers who are interested in bountiful muskrat harvests are in favor of surcharging or raising water levels on marshes in fall to ensure adequate depths for substantial overwinter survival of muskrats. Landowners are often concerned with seeding their crops as early as possible, and want marsh levels lowered in preparation for spring runoff. Biologists are often in the middle, trying to do what is best for a balanced marsh ecosystem.

Lack of difference in population levels and overwinter survival among water-level treatments would indicate that, in the early stages after a drawdown at least, it is not necessary to surcharge marshes to ensure overwinter survival. This is appealing because fall surcharging can be expensive to implement when water is not readily available.

This study also supports the premise that stable water levels over the short term results in increasing populations of muskrats. Although draining wetlands to promote growth of vegetation (Kadlec 1962, van der Valk and Davis 1978) can leave muskrats stranded (Bellrose and Low 1943), wetland managers should not be afraid to implement drawdowns for fear of losing potential fur harvest. Results from the MERP study indicate that, at most, 2 years of harvest would be lost. If drawdowns were implemented on a rotating schedule between adjacent marshes, the lost harvest would easily be compensated by improved returns later. The rapid recolonization of the MERP cells following drawdown is especially remarkable considering the low muskrat densities in the surrounding Delta Marsh.

In Manitoba, muskrats are harvested during spring break-up, when animals are larger and have a greater value per pelt. However, Clark (1987) showed that harvest and nonharvest mortality are compensatory; thus spring trapping results in lost opportunity for harvest. The present study shows that muskrats are able to counteract low overwinter survival with greater rates of increase the following spring. In addition, Parker and Maxwell (1984) concluded that spring harvest often results in lower income as pelts are often damaged from intraspecific fighting. Fall-harvested muskrats, although smaller and of poorer grade, are more plentiful and may produce higher total income for fur harvesters.

Wetland managers now have the data to do some very fine-tuned management of muskrats. Information is available on response of dynamics to different management practices and to different population densities. The fall harvest can be regulated by the timing of the trapping season (Clark 1986). Responses of wetland vegetation to drawdowns has been documented (van der Valk and Davis 1978, Pederson 1981). By manipulating water levels and regulating fall harvest, the potential is there to achieve the desired result of sustained, high levels of fur harvest with the benefits of wetland interspersion brought about by the interactions of muskrats and wetland vegetation.

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